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EPIPHYTES AND CLIMATE CHANGE RESEARCH IN THE CARIBBEAN: A PROPOSAL

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"Licht, feuchte Luft, reichliche Thaubildung, häufige Regengüsse stellen die wesentlichen Bedingungen eines üppigen epiphytischen Pflanzenlebens dar, und wo sie sich in hohem Grade vereinigt finden, wie in gelichteten Bergurwälderns, und in Galleriewäldern grosser Flüsse, zeigt sich die epiphytische Vegetation in vollster Pracht und grösstem Formenreichthum." (Schimper, 1888, p. 90)

("Light, humid air, abundant dew formation, frequent rains, represent the essential conditions for a lush development of epiphytic life, and where they are found in high degree, as in well illuminated pristine montane forests, and in gallery forests of large rivers, the epiphytic vegetation reaches maximum development and variety of forms.")

ABSTRACT. The purpose of this paper is to call attention to the importance of epiphytes in understanding how global atmospheric changes impact tropical forests. The Luquillo Experimental Forest (LEF), like other peaks in the Caribbean, intercepts at least five major global weather systems: (1) trade winds originating in the Azores; (2) tropical depressions and hurricanes originating in western Africa; (3) northern cold fronts originating in the polar regions of North America; and systems originating (4) in the Pacific and (5) the Amazon basin. Each of these "global airsheds" has a particular return frequency, associated temperature and climatic conditions, and different chemical conditions in rain and cloud water. Epiphytes are the organisms with the closest interactions with these systems because they absorb water and nutrients directly from the atmosphere and their metabolism responds to prevailing conditions associated with each airshed. In order to detect effects of global change on epiphyte communities, it will be necessary to build a long-term quantitative record of ecological information of these organisms. In this paper, we review the information available for the LEF and outline our proposed program to measure ecosystems effects of global change via epiphytic communities. Our focus will be on biomass accumulation, nutrient uptake, and hydrological fluxes.

Investigaciones sobre epífitas y cambios climáticos en el caribe: una propuesta

RESUMEN. Este artículo tiene el propósito de llamar atención a la importancia de las plantas epifíticas para entender como los cambios atmosféricos globales impactan los bosques tropicales. El Bosque Experimental de Luquillo (BEL), al igual que otros picos del Caribe, intercepta por lo menos cinco sistemas atmosféricos principales: (1) los vientos alisios con origen en las Azores, (2) depresiones tropicales y huracanes con origen en la costa oeste de Africa, (3) frentes fríos con origen en las regiones polares de Norte America, y otros sistemas con origen (4) en el Amazonas y (5) en el Pacífico. Cada uno de estos sistemas climáticos tienen sus propias periodicidades, temperaturas, climas asociados, y diferentes condiciones químicas en sus aguas de lluvia o en las nubes. Las epífitas son organismos que dependen de estros sistemas porque absorben el agua y los nutrientes directamente de las nubes o la lluvia y estan expuestas a las condiciones asociadas a cada sistema. Para detectar el efecto de cambios globales con el estudio de comunidades epifíticas, es necesario desarrollar información cuantitativa a largo plazo sobre la ecología de estos sistemas. Aquí revisamos la información disponible para el BEL y desarrollamos una propuesta para un programa de estudio sobre este tema. Nuestro foco es la producción y acumulación de biomasa, ciclaje de nutrientes y flujos hidrológicos.

INTRODUCTION

Epiphytes attracted the attention of early botanists such as Schimper (1888, 1903) and today, several generalizations about the distribution, physiology, and ecology of these plants are evident. Epiphytes: (1) occur in greatest abundance in wet and rain forest (*sensu* Holdridge, 1967) environments (Schimper, 1888), (2) predominate in the New World tropics, (3) account for a large fraction of the species richness of many wet and rain forests (Gentry & Dodson, 1987), (4) are generally adapted to obtaining their mineral nutrition from sources other than ground-level mineral soil or exclusively from the atmosphere (Benzing, 1990), and (5) have a positive influence on ecosystem processes, particularly in the support of foodchains, enhancement of biodiversity and nutrient use-efficiency, and re-distribution of moisture (TABLE 1).

TABLE 1. Epiphytes and the tropical forest. Based on Benzing (1990), Forman (1975), Gentry and Dodson (1987), Weaver (1972a), Brown *et al.* (1983), and Lugo (1986).

Account for a large fraction (up to 50%) of the total plant species richness.
Support a very large diversity of insects.
Contribute to a large fraction of the Leaf Area Index of crowns.
Enter in numerous types of symbiotic relationships with other organisms, e.g., ants, frogs, birds.
Have unique mechanisms to acquire essential ions.
Some groups are in active state of evolution.
Contribute significantly to forest nutrient cycles and productivity.
Enhance nutrient-use efficiency of the forest.
Capture and store nutrients from atmospheric sources.
Form new substrates, including organic humus, available to other organisms.
Concentrate organic and inorganic resources that would otherwise be diluted in the wet and rain environment.
Support organisms that fix N or they themselves fix N (e.g., microepiphytes).
Provide an aquatic habitat and high humidity for many organisms.
Impound large amounts of water in the canopy and redistribute throughfall and stemflow.
Many birds are epiphyte-dependent for a large fraction of their needs.
Affect other plants in the community by a number of mechanisms, including competition for light and nutrients, mechanical effects, and parasitism.

While there is a wealth of information on mineral nutrition and ecophysiology of epiphytes, less scientific attention has been given to ecosystem-level attributes of epiphytic organisms. For example, there are only few estimates of biomass accumulation (TABLE 2) and no estimates of primary productivity for the epiphyte component of tropical forests. Available information on epiphyte photosynthetic and transpiration rates per unit area show a wide range of values and document both C-3 and CAM pathways (Griffiths *et al.*, 1986; Lüttge *et al.*, 1986a, 1986b; Smith *et al.*, 1986a, 1986b; Benzing, 1990). Without ecosystem-level information on these organisms, however, it is impossible to fully understand their ecological role and the functioning of wet and rain forests.

In this paper, our objective is to present a proposal for climate change research in the Neotropics, using cloud forests and epiphytes as biotic indicators of change in atmospheric conditions. We focus attention on the rationale for our study, the characteristics of epiphyte communities in the Luquillo Experimental Forest (LEF), and a hypothesis on how epiphytic communities influence ecosystem function.

Rationale for Global Change Research in the Caribbean

The Caribbean Basin is influenced by five major global weather systems, i.e., (1) easterly trade winds originating in the Azores, (2) tropical depressions and hurricanes originating off the west coast of Africa or in west Africa, (3) northern cold fronts originating in the higher latitudes of continental North America, (4) air masses originating in the Amazon Basin, and (5) air masses originating in the Pacific (FIGURE 1). Each of these "global airsheds" has a particular return frequency, associated temperature and climatic conditions, and quality of rain and cloud water (TABLE 3).

Available data suggest that inputs of essential nutrients in rainfall and cloud water to the biota are significant (TABLE 4). Saharan dust alone is believed to transport sufficient P to support the primary productivity of the Caribbean Sea (Prospero *et al.*, 1981; Prospero & Nees, 1989; Talbot *et al.*, 1986). Studies of cloud and rain water chemistry on the East Peak of the LEF and elsewhere in the United States show that mean concentrations of H^+, NO_3^-, and SO_4^{-2} are three to seven times higher in cloud water than mean concentrations in rain (Weathers *et al.*, 1988). In some locations, cloud input can be as important as rain in terms of cumulative effects on vegetation. In the terrestrial environment, epiphytes are the organisms with the closest interaction with these atmospheric systems because they absorb water and nutrients directly from the atmosphere and their metabolism responds to prevailing conditions associated with each airshed (Medina, 1986).

In order to detect effects of global change on epiphyte communities, it will be necessary to build long-term quantitative records of ecological information of these organisms and their atmospheric environments. Moreover, it will be necessary to associate instantaneous environmental conditions regulating epiphyte metabolism to specific atmospheric systems. Such research combines small-scale ecophysiological work with large-scale studies of weather and ecosystem-level responses.

Use of Geographic Information Systems (GIS) will be necessary to properly interpolate and extrapolate results of point studies to larger spatial scales. Point studies should be scattered throughout the region as a coordinated network of study areas (FIGURE 1).

The use of epiphytes as indicators of atmospheric change is not new. The documentation of epiphyte retention of fallout originating over continental areas from aboveground explosions of nuclear devices provides empirical evidence for the connection of global airsheds with epi-

TABLE 2. Biomass of epiphytes in various ecosystems. Luquillo Experimental Forest is LEF.

Ecosystem and location	Biomass (Mg/ha)	Source
Temperate		
Bukk Mountains, Hungary	0.043	Simon, 1974 in Smith, 1982
Rain forest Olympic National Park Hoh River Valley, USA	6.8	Grier & Nadkarni, 1987
Tropical		
Cloud forest San Eusebio, Venezuela	3.84	Brun, 1976 in Medina, 1986
Cloud forest Monteverde, Costa Rica	4.7	Nadkarni, 1984
Cloud forest, Pico Oeste LEF, P.R.	5.0	Lyford, 1969
Mossy elfin forest Uluguru Mountains, Tanzania	13.6	Pócs, 1982
Lower montane rain forest New Guinea	3.4	Edwards & Grubb, 1977
Submontane forest Uluguru Mountains, Tanzania	2.13	Pócs, 1982
Lower montane wet forest LEF, P.R.	0.5*	Weaver & Murphy, 1990
Lower montane wet LEF, P.R.	2.0–4.0	Frangi & Lugo, 1985, 1992
Premontane forest Darién, Panama	1.4	Golley *et al.,* 1971
Moist forest, Manaus, Brazilian Amazon	0.05	Klinge *et al.,* 1975
Dry forest, Guánica, P.R.	0.14	Murphy & Lugo, 1986

* Estimated from Leaf Area Index.

phyte communities in the Caribbean (Odum *et al.,* 1970). An extensive literature describes the role that epiphytes have played in the detection of air pollution (Smith, 1982; Rao, 1982). Most studies have focused on the presence or absence of species, or the accumulation of heavy metals in their tissues as measures of pollution effects. We propose to use these techniques and also to measure the movement of atmospheric constituents into the epiphytic biota and the subsequent transfer to the rest of the ecosystem via food-chains and hydrological fluxes. We will also use epiphyte metabolism, phenology, and growth as indicators of climate change. Our goal is to understand how epiphytes function at the interface between the atmosphere and within the rest of the ecosystem.

Epiphyte Communities in the Caribbean

Epiphytic communities are common at all elevations and climates in the Caribbean. Plant endemism increases in cloud forests (Lewis, 1971). An overview of the cloud forests that support epiphytic communities was recently published by Stadtmüller (1987). High density of epiphytes was described at sea level in the Guánica dry forest by Murphy and Lugo (1986) who associated their abundance with night fog of marine origin (TABLE 2). However, epiphytes increase in abundance with elevation and generally reach maximum richness of species and biomass in cloud forests (Benzing, 1990; TABLE 2).

Cloud forests are believed to be the most structurally complex of all terrestrial ecosystems, in part due to the diversity of epiphytes (Vareschi, 1986). They are also considered endangered ecosystems because of their small area and the unregulated development of mountain peaks (LaBastille & Pool, 1978). Fortunately, cloud forests have been studied in some detail in the Caribbean basin, e.g., Pico del Oeste (Journal of the Arnold Arboretum, 1968–1977), and Pico del Este (e.g., Weaver, 1972a, 1972b; Byer & Weaver, 1977; Medina *et al.,* 1981; Weaver *et al.,* 1986), Puerto Rico; Rancho Grande, Venezuela (Huber, 1986); Monteverde, Costa Rica (e.g., Nadkarni, 1984); LaSoufrière, Guadeloupe (Fritz-Sheridan & Portécop, 1987); Sierra de las Minas, Guatemala (Catling & Lefkovitch, 1989); Massif de la Hotte, Haiti (e.g., Curtis, 1946); and the Blue Mountains, Jamaica (e.g., Tanner, 1977). These studies provide considerable insight into cloud forest ecology and the role of epiphytes.

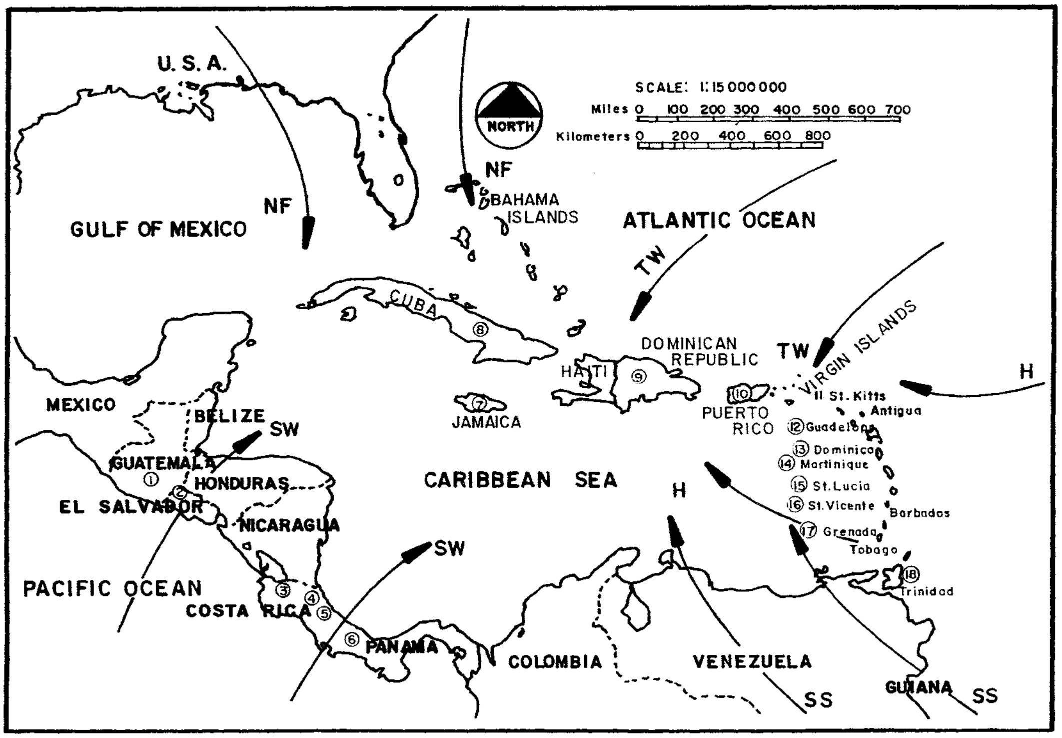

FIGURE 1. Map of the Caribbean illustrating the major weather systems that converge on the region and their origins (airsheds). Also illustrated are the location of major cloud forests that could form a network of research sites to elucidate the relationship between global airsheds and the biota. The original map of cloud forest sites was developed by LaBastille and Pool (1978). The numbers identify specific sites as given by LaBastille and Pool. 1. Quetzal Cloud Forest Reserve, Guatemala; 2. Montecristo National Park (proposed), El Salvador; 3. Monteverde Cloud Forest Reserve, Costa Rica; 4. Volcano Poas National Park, Costa Rica; 5. Volcano Chirripó National Park, Costa Rica; 6. Volcano Barú National Park, Panama; 7. Blue Mountain Peak, Jamaica; 8. Pico Turquino, Cuba; 9. Armando J. Bermúdez-National Park, Dominican Republic; 10. Caribbean National Forest and Commonwealth Forests, Puerto Rico; 11. Mt. Misery, St. Kitts; 12. Soufrière, Guadeloupe; 13. Morne Trois Pitons National Park, Dominica; 14. Mt. Pelee, Martinique; 15. Mt. Gimie, St. Lucia; 16. Soufrière, St. Vincent; 17. Mt. St. Catherine, Grenada; 18. El Aripo, Trinidad.

We propose to build on this information by studying these ecosystems in the context of particular global airsheds and how epiphytes link global phenomena to whole forest ecosystem function.

Influence of Epiphytes on Ecosystem Function

A common practice in comparative ecology is to characterize ecosystem biomass, leaf area index, nutrient distribution, relative species composition, and distribution of life forms of various plant and animal groups to compare the relative magnitude of these parameters. In these investigations, epiphytes are usually ranked low in comparison to trees (TABLES 5, 6) although Nadkarni (1984) showed that up to 45% of the foliage nutrient pool in a cloud forest was stored in epiphytes. Benzing (1980, 1990) suggested that the absolute value of structural or functional parameters are not as important as the influence of organisms in the functioning of the whole ecosystem (TABLE 1).

We propose that the importance of groups of organisms to ecosystem function be evaluated in the context of the ecosystem sector or biotic-abiotic interface in which they function. This is illustrated in FIGURE 2, which depicts a model of how we interpret the function of components in a wet forest in the LEF. The model shows seven interfaces between the forest biota and the environment. At each of these interfaces, groups of organisms function and influence nutrient-use efficiency and organic matter turnover (TABLE 7). Different life forms occupy different interfaces. For bryophytes, this can be illustrated by the diversity of life forms and surfaces where these

TABLE 3. Conditions associated with the three major weather systems that drive the ecosystems of the Luquillo Experimental Forest. Compiled from McDowell *et al.* (1990), Prospero *et al.* (1981), Prospero and Nees (1989), Savoie *et al.* (1989), and Jickells *et al.* (1982).

Weather system	Prevailing conditions
Northeastern trades	Steady wind direction, speed, and air temperatures. Responsible for localized daily orographic rains and rainshadows. Precipitation chemistry dominated by sea salt aerosols.
Systems originating in eastern Atlantic or Africa	Low pressure systems and hurricanes with high intensity, long duration, and widespread rainstorms. Predominantly occur in summer and fall. Cloudy opaque atmosphere with low light intensities. Precipitation chemistry influenced by Saharan dust and has high concentration of Ca, Mg, K.
Northern fronts	Winter time influence, lower temperatures, higher SO_4^{-2} and NO_3^- input by rainfall, periodic wind storms.

plants grow (TABLE 8). The absolute value of structural and functional parameters at these interfaces is a function of environmental conditions at the interface, rather than a function of the importance of that ecosystem sector.

Interfaces exposed to high availability of resources (e.g., nutrients, water) and non-stressful conditions (e.g., optimal temperature, humidity) usually have high rates of flux across the environment-biotic interface. The net accumulation of biomass in the biotic component depends on the rates of export from the biota and the frequency of disturbances, i.e., accumulation of nutrients or biomass can be either high or low. Examples are the soil-litter interface and the canopy-atmosphere-soil interface. Both of these interfaces operate at rapid metabolic rates but the latter supports conspicuous leaf compartments while the former supports microscopic fungi, bacteria, and microinvertebrates. Surprisingly,

TABLE 5. Leaf area index of the *Cyrilla racemiflora* and *Dacryodes excelsa* (tabonuco) forests in the Luquillo Experimental Forest, Puerto Rico (Weaver & Murphy, 1990; Odum, 1970).

	Cyrilla		Tabonuco	
Leaf component	Leaf area index	% of total	Leaf area index	% of total
Epiphytes	0.30	6	0.01	0.1
Herbs, seedlings and/or grasses	1.18	24	1.03	14
Bryophytes	0.47	9	0.06	0.8
All other plants	3.01	61	6.24	85
Total	4.96	100	7.34	100

leaf biomass in the LEF is similar to fungal, bacterial, and microinvertebrate biomass (J. Lodge, pers. comm.; Lugo & Scatena, 1993). Interfaces between aerobic and anaerobic conditions or aquatic-terrestrial environments are characterized by harsh environments (e.g., low oxygen concentration or turbulent medium) and low rates of flux across the biotic-abiotic boundary. Regardless of rates of flux or magnitude of accumulation of nutrients and biomass, the relative importance of each group of organisms is that they allow the function of, and contribute useful work from the interaction to, a given abiotic interface.

Epiphytes function in the atmospheric-terrestrial interface (FIGURE 2). Cloud water can contribute as much mineral input as rain water at this interface. With healthy epiphytic communities, cloud forest ecosystems have the benefit of nutrient and organic matter fluxes originating at this interface. Without epiphytes, these inputs could be lost because clouds would pass through without being intercepted, or if root uptake could not keep up with the high amount of water passing through the system. These ecosystems would then be less productive, with less efficiency in the use of resources, and thus, less biologically active and resilient. Because of this coupling between environment and biota, any global climate or atmospheric change should be reflected first in the epiphytes of cloud forests.

TABLE 4. Estimated annual nutrient inputs to Caribbean tropical forests from rain and clouds.

	Input (kg/ha·yr)					
Ecosystem	N	P	K	Ca	Mg	Source
Cloud forest, Central Costa Rica	14.5	2.0	6.0	5.0	2.0	Benzing, 1990
Subtropical wet forest, Luquillo Experimental Forest, Puerto Rico	2.2		3.3	11.4	7.7	McDowell *et al.*, 1990

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